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NESTING BIOLOGY AND DIET OF THE MADAGASCAR HARRIER (*CIRCUS MACROSCELES*) IN AMBOHITANTELY SPECIAL RESERVE, MADAGASCAR

LILY-ARISON RENE DE ROLAND, JEANNENEY RABEARIVONY, AND IGNACE RANDRIAMANGA
The Peregrine Fund's Madagascar Project, B.P. 4113, Antananarivo (101), Madagascar

RUSSELL THORSTROM[1]
The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, ID 83709 U.S.A.

ABSTRACT.—We studied Madagascar Harriers (*Circus macrosceles*) in the central high plateau at Ambohitantely Special Reserve, Madagascar during the 1997 and 1998 breeding seasons. We located 11 nests and documented eight nesting attempts during the two seasons. All nests were placed on vegetation within marshes (N = 9) and averaged 43 cm above water level. Breeding commenced in late August and September, during the middle of the dry season. Egg laying occurred from the middle of September to the end of October, peaking in late September and spanning 40 d for eight clutches. The incubation period was 32–34 d at eight nests and nestlings fledged at 42–45 d of age (N = 7) in November and December, at the start of the rainy season. Of 23 eggs laid in eight nests ($\bar{x}$ clutch size = 2.9), 17 of 23 (74%) hatched, and seven (41%) of those hatchlings fledged. Overall productivity was 0.9 young fledged per breeding attempt and nest success was 75% (N = 8). Only one of six successful nesting attempts fledged two young. The Madagascar Harrier diet from 272 identified prey was composed of insects (48%), snakes (21%), birds (21%), lizards (6%), rodents (3%), and domestic chickens (1%); in terms of biomass based on prey remains and pellets: birds (45%), reptiles (35%), and mammals (18%) made 98% of prey. This is the first breeding study of this species, and it shows this harrier reproduces at a relatively low rate, and has an unusual diet relative to related species.

KEY WORDS: *Madagascar Harrier*; Circus macrosceles; *Madagascar*; *nests*; *diet*; *nesting behavior*.

DIETA Y BIOLOGIA DE ANIDACION DE *CIRCUS MACROSCELES* EN LA RESERVA ESPECIAL DE AMBOHITANTELY, MADAGASCAR

RESUMEN.—Estudiamos los aguiluchos de el Madagascar (*Circus macrosceles*) en la Reserva Especial de Ambohitantely, Madagascar durante las estaciones reproductivas de 1997 y 1998. Localizamos 11 nidos y documentamos ocho intentos de anidacion durante las dos estaciones. Todos los nidos fueron ubicados en vegetación de pantano (N = 9) y promediaron 43 CMS sobre el nivel del agua. La reproducción comenzó a finales de Agosto y Septiembre, a mediados de la estación seca. La postura de huevos ocurrió desde mediados de Septiembre hasta finales de Octubre, con un pico hasta finales de Septiembre y expandiéndose por 40 días y eight nidadas. El periodo de incubación fue de 32–34 días en ocho nidos y los pichones emplumaron a los 42–45 días de edad (N = 7) en Noviembre y Diciembre, al inicio de la estación lluviosa. De los 23 huevos puestos en eight nidos (tamaño de la nidada = 2.9) 17 de 23 (74%) eclosionaron y seven (41%) de los pichones emplumaron. La productividad general fue de 0.9 pichones emplumados por intento reproductivo y el éxito de anidacion fue de 75% (N = 8). En solo uno de seis intentos exitosos de anidacion emplumaron dos pichones. La dieta del aguilucho de Madagascar (de 272 items de presas identificadas) estuvo compuesta por insectos (48%), Serpientes (21%), aves (21%), lagartijas (6%), roedores (3%) y gallinas domesticas (1%). En términos de biomasa, con base en restos de presas y egagropilas las aves constituyeron un 45%, los reptiles un 35% y los mamíferos un 18% para un total de un 98% de presas. Este es el primer estudio sobre la reproducción de esta especie y muestra que el aguilucho se reproduce a una tasa lenta y tiene una dieta inusual comparada con las de las especies relacionadas.

[Traducción de César Márquez]

[1] Corresponding author's e-mail address: rthorstrom@peregrinefund.org

Our knowledge of the ecology and biology of Malagasy raptors has gradually increased based mostly on research in northeastern Madagascar (Thorstrom and Rene de Roland 2000); however, the biology of the Madagascar Harrier (*Circus macrosceles*) is still poorly known. The cosmopolitan group, the harriers (*Circus*), is relatively well-known 16 species of medium-sized hawks, and includes one species in Madagascar. This harrier (*C. macrosceles*) was recently separated and elevated to a full species rank by M. Wink in Simmons (2000), based on DNA evidence and morphological differences from its sister species, the Réunion Harrier (*C. maillardi*; Bretagnolle et al. 2000). The Madagascar Harrier is a rather uncommon bird of the open marshes and grasslands, and is observed infrequently coursing over grass fields, fallow rice fields, marshes, and wetlands (Langrand 1990, del Hoyo et al. 1994). Globally, it is classified as a vulnerable species (BirdLife International 2000). Its diet consists predominantly of birds, reptiles, mammals, and insects (Rand 1936, Langrand 1990). Threats to this species include dry season grassland fires that usually occur during its nesting season, loss of marsh and grassland habitat, and human persecution to protect poultry and for food (Paverne 1997, BirdLife International 2000). The population status and distribution is not well known. Here, we provide new information on the breeding biology of the Madagascar Harrier from the high central plateau region of north-central Madagascar.

STUDY AREA

We studied the Madagascar Harrier in Ambohitantely Special Reserve (18°13′S, 47°16′E) and its surrounding area during two consecutive breeding seasons, 1997–98 (Randriamanga 2000). This reserve is situated in the high central plateau, about 130 km northwest of Antananarivo, the capital of Madagascar. In 1982, the area was classified as a Special Reserve of 5600 ha (Nicoll and Langrand 1989). Of the 5600 ha, only 2800 ha are still covered by native forests, 1960 ha by grasslands including marshes, and 840 ha of exotic plantations (Langrand 1995). The eastern-facing slopes contain the native forest fragments. In the higher elevations and the western section of the reserve, the area is covered by grasslands composed of *Aristida rufescens, Loudetia* sp., and *Andropogon* sp., and low-lying areas of marshes with other grasses and reeds (e.g., Cyperaceae). On the knolls and summits in the western section, small stands of introduced trees of *Pinus patula* and *Eucalyptus* sp. are common. The elevation varies from 1267–1660 m. The climate is characterized by two distinct seasons; a dry warm period from April–October and a hot rainy season from November–March. The mean annual rainfall is 2150 mm and seasonal temperatures range from 10–25°C (Nicoll and Langrand 1989).

METHODS

We searched marshes, valleys, and rolling hills over the whole reserve daily from July–December 1997 and August 1998–January 1999 for potential breeding pairs. We watched for harriers flying near marshes to detect pair activities and courtship behavior. We followed harriers daily by sight until a nest was confirmed by a pair's behavior or by locating the nest. Nest observations were made from the ground with 10× binoculars and 20–45× spotting scope at distances of 200 m. We observed nest sites from 0500–1830 H and rotated among nests. When accessible, we measured nest length, width, and height above water level to the nearest 1.0 cm. We considered the incubation period to be the time (d) from the laying of the penultimate egg (usually the second or third laid egg) to the hatching of the second egg (Simmons 2000) We measured length and breadth of eggs to the nearest 0.1 mm with vernier calipers and fresh egg mass to the nearest gram with a 100 g Pesola spring scale (Pesola, Jackson, MS U.S.A). Reproductive variables and productivity were defined as: breeding attempt (nests that contained at least one egg), laying date (when the first egg was laid), clutch size per individual nest (number of eggs laid in nests), mean clutch size (mean number of eggs laid per breeding attempt), number of eggs hatched, young fledged (number of young surviving to first flight), productivity (number of young fledged per breeding attempt), and nest success (number of total breeding attempts that fledged at least one young).

Prey delivered by adults was identified and quantified during daily nest observations. Prey remains were collected from nests and were identified by S. Goodman of World Wide Fund for Nature (WWF) in Madagascar. Madagascar Harriers were trapped with a bal-chatri placed near the pair's center of activity during the breeding period (Thorstrom 1996). We determined body mass with a 1000 g Pesola spring scale and measured wing and tail length to the nearest 0.1 mm with vernier calipers or to the nearest 1 mm with a metric tape measure. Three birds were color banded for individual identification.

RESULTS

Courtship activities began in August and September. Initiation of the breeding season began with courtship flights and pairs defending a space around a site, where they intended to place a nest. We located seven nest sites in 1997 and four in 1998, of which two were on the same territories as 1997, (total of nine sites in an area ca. 1500 ha; Fig. 1). The distance between neighboring nests averaged 1514.5 m ± 674.6 m (range = 370–3720 m, $N = 9$ pairs).

Courtship Behavior. Courtship behaviors consisted of intraspecific vocalizations, aerial display flights by males, pair-formation flights, nest building activities, courtship feedings, copulations, and

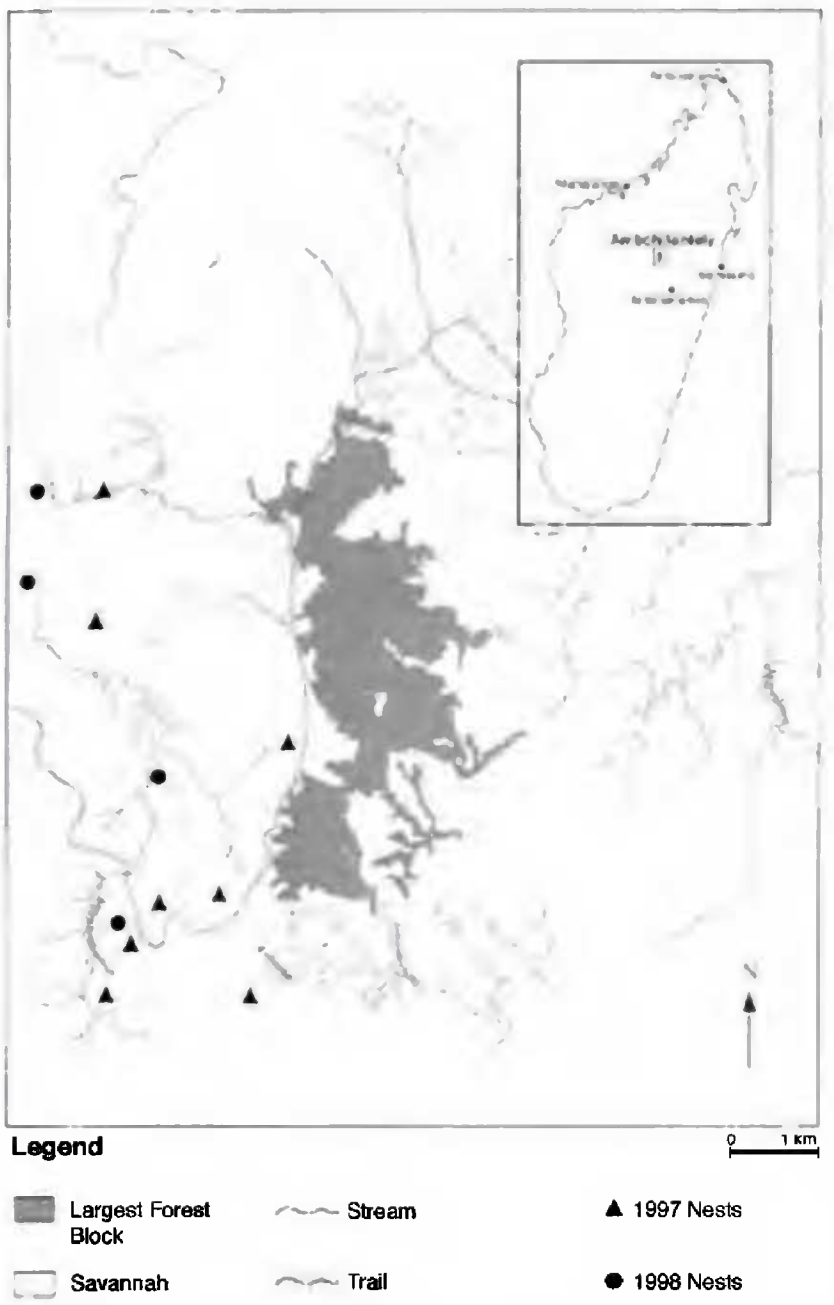

Figure 1. Location of study site, Ambohitantely Special Reserve, in Madagascar and nest locations during 1997 and 1998 breeding seasons.

nest defense. Aerial display flights began with a spiraling, ascending flight by the male, then progressed to a fast hard flapping flight with steep undulations and then to rapid descending spirals with "koue" vocalizations. The earliest pair-formation flight observed was on 12 August 1997. Pair-formation flights involved the male and female flying slowly together in their territory and sometimes stalling and grabbing at the other member of the pair. Males called "koue . . . koue" every 10–15 sec during pair-formation flights. During the courtship period the female was provisioned with food by the male. Copulations always came after a prey delivery from male to female. Copulations averaged 8.9 ± 0.9 (SE) sec in duration (N = 12, range = 6–15 sec) and occurred 3–4 times a day.

The territorial defense call may be described as "ouek" given ca. 5 sec when another harrier was close to the nesting area. Also, "kêkêkêkêkê" was the sign of alarm or emitted when a predatory animal was close to the nest.

Three adults were trapped during this period. Measurements taken were: wing chord = 459 mm, 461 mm, and 443 mm; and tail = 288 mm, 285 mm, and 272 mm, for two females and one male, respectively. Madagascar Harriers show moderate reverse size dimorphism. The mass of two females were 850 and 910 g and the one male was 600 g.

Nest Building. Nest construction began 15–17 d after pair formation. The earliest nest building was observed on 26 August 1997. The male was predominantly responsible for building (quantitative data not available) the nest, while the female remained in the nest vicinity vocalizing for food. All nests were built on vegetation in marshes. Herbaceous vegetation and grasses used in nest building were collected from the ground (e.g., *Eulalia villosa, Osmunda regalus, Scirpus* spp., *Kotschya africana, Aristida rufescens,* and *Pteridium* spp.), while dry twigs were collected from *Eucalyptus* and *Pinus* trees. All nesting material was collected from 40–200 m of the nest site.

Nest building activities started early morning, from 0530–0900 H, and continued again from 1700 H–sunset. Due to the level of water below nests, only nine of 11 located nests were accessible for measurements. Nest measurements averaged 63.2 ± 7.2 cm (range = 50.0–77.0 cm) by 44.5 ± 4.5 cm (range = 34.2–51.3 cm). For nine nests, the mean height above water was 43.2 ± 15.5 cm (range = 24.5–81.0 cm). Pairs built new nests every year and the mean distance between the previous year's nest in a given territory was 575 m ± 205.1 m (N = 2). Nest building took 25–30 d (N = 11 nests). A renesting attempt occurred at one nest 200 m from the first nest which was destroyed during the early incubation period.

Egg Laying. During the two breeding seasons, the earliest recorded laying date was 13 September 1997 with incubation starting on 15 September 1997 and the latest laying date was 20 October 1997 with incubation starting on 26 October 1997 (N = 8 nests). The modal clutch size was three (N = 5), followed by clutches of two (N = 2), and there was one four-egg clutch; the mean clutch size was 2.9 ± 0.2. Mean dimensions of 23 Madagascar Harrier eggs were 48.7 ± 1.7 mm (44.1–51.0 mm) by 37.5 ± 1.1 mm (35.7–40.0 mm). Mean fresh egg mass was 36.5 ± 1.2 g (34.8–39.0 g).

Incubation. Only females incubated. In 216.3 hr

Table 1. Reproductive success of Madagascar Harriers (*Circus macrosceles*) at Ambohitantely Special Reserve, Madagascar, during the breeding seasons of 1997 and 1998.

YEAR	NESTS	BREEDING ATTEMPTS OBSERVED	NUMBER OF EGGS	MEAN CLUTCH SIZE	NO. EGGS HATCHED (%)	NO. YOUNG FLEDGED (%)	FLEDGLINGS/ BREEDING ATTEMPT	NEST SUCCESS (%) (*N*)
1997	7	4	12	3	10 (83%)	4 (40%)	1.00 (4/4)	100 (4)
1998	4	4	11	2.7	4 (37%)	3 (75%)	0.75 (3/4)	50 (2)
Total	11	8	23	2.9	14 (61%)	7 (50%)	0.88 (7/8)	75 (6)

of nest observations, females incubated for 196.8 hr (91%) and the nest was unattended for 19.5 hr (9%). The incubation period ranged from 32–34 d ($N = 8$ nests). During the incubation period, the male's primary role was food provisioning to the female and nest defense.

Nestling Period. At hatching, nestling mass varied from 25–32 g ($N = 6$). Brooding and feeding the young was the female's responsibility. When the male arrived with prey, he circled above the nest, and called "tou . . . tou . . . touff" to the female. Also, the female solicited food by calling "kiou . . . kiou . . . kio . . . ." Prey were delivered directly to females mostly by an aerial transfer (88.8%; $N = 166$). In several instances, when the female did not respond to the male and leave the nest or was absent, the male delivered the prey directly into the nest (11.2%). The earliest the female was observed leaving the nest and hunting for the nestlings was when the nestlings were 24 d of age. Young first flew from 42–45 d of age ($N = 7$). First flights of young were about 1–5 m from the nest.

Post-fledging Period and Dispersal. By 48 d of age, young were flying 20 m from the nest. Fledglings were always fed at the nest by the adults during the first week. At 50 d of age, the male tried transferring food to the young in flight while the female placed prey on tufts of grass averaging 136.7 ± 101.7 m ($N = 6$, range = 40–300 m) from the nest. After 50 d of age, young were not observed being fed by the females and solicited food with the "kiou" call. At 55 d of age, young flew up to a height of 100–200 m and did not return to their nests for periods of ca. 15 min. Fledglings began taking prey in flight from the male at 55 d of age. The adult females had disappeared from their nesting territories when young were ca. 65 d of age ($N = 7$ nests). Young dispersed from their natal areas at 70 d of age along with the adult male.

Reproductive Success. In eight fully-monitored nests containing 23 eggs, 14 (61%) hatched, and seven (50%) of those hatched fledged (Table 1). In total, seven young fledged from eight breeding attempts, for an overall productivity of 0.9 young fledged. Nest success for the 2 yr of the study was 75% ($N = 8$). In 1998, two nests were destroyed by a grassland fire during incubation. Reproductive losses resulted from brood reduction (59%), addled eggs (26%), and Pied Crows (*Corvus albus*; 15%) among the eight nesting attempts. For each nest containing three young, the third individual was always dead at less than 10 d of age. In nearly all nesting attempts with two or more young, the second nestling hatched did not survive more than 40 d, and was often dead between 14–35 d of age. Only one of eight nesting attempts was successful in fledging two young.

Food Habits. We observed 272 prey items being delivered to females and nestlings during the two study seasons. On a numerical basis, insects were the predominant prey comprising 48.2% ($N = 131$) of the diet, followed by snakes 20.9% ($N = 57$), birds 20.6% ($N = 56$), chameleons (*Furcifer* spp.) 5.9% ($N = 16$), rodents 3.3% ($N = 9$), and chickens (*Gallus gallus*) 1.1% ($N = 3$). Prey remains ($N = 12$) and pellets ($N = 22$) left in the nests were identified and composed of 24% insects, 44% birds, 14% snakes, 6% chameleons, and 12% rodents and insectivores ($N = 50$ identified prey; Table 2). On a biomass basis, birds (44.7%), reptiles (35.6%), and mammals (18.6%) comprised 98.9% of the estimated biomass from prey remains and pellets (Table 2).

DISCUSSION

In this first ecological study of the breeding and diet of the Madagascar Harrier we found: nesting was limited to marshy areas of savannah habitat in Ambohitantely Special Reserve, breeding commenced in the spring (August–September) similar to other southern harriers, copulations were always

Table 2. List of prey species identified from remains and pellets of Madagascar Harriers (*Circus macrosceles*) at Ambohitantely Special Reserve, Madagascar during 1997–98.

PREY SPECIES	NO. ITEMS	BIOMASS (G)	BIOMASS TOTAL (%) AND SOURCE
INSECTS		60	1.1
Orthopteran (*Nomadacris septemfasciata*)	12	5	Estimate[a]
REPTILES		1850	35.6
Chameleon (*Furcifer lateralis*)	3	150	Estimate[a]
Snake (*Liopholidophis lateralis*)	7	200	Estimate[a]
AVES		2325	44.7
Madagascar Flufftail (*Sarothrura insularis*)	1	300	Dunning 1993
Common Quail (*Coturnix Coturnix*)	2	100	Dunning 1993
Madagascar Partridge (*Margaroperdix madagascarensis*)	4	220	Dunning 1993
Madagascar Button-quail (*Turnix nigricollis*)	1	40	Estimate[a]
Common Stonechat (*Saxicola torquata*)	2	15	Dunning 1993
Madagascar Lark (*Mirafra hova*)	3	45	Estimate[a]
Madagascar Cisticola (*Cisticola cherinus*)	1	10	Dunning 1993
Domestic chicken (*Gallus gallus*)	3	300	Estimate[a]
Unidentified birds	5		
MAMMALS		965	18.6
Black Rat (*Rattus rattus*)	4	200	Garbutt 1999
House Mouse (*Mus musculus*)	1	15	Garbutt 1999
Lowland-streaked Tenrec (*Hemicentetes semmispinosus*)	1	150	Garbutt 1999
TOTAL	50	5200	

[a] Based on mass measurements taken in the field.

accompanied by prey delivery by males, clutch was typically small (2.9 eggs) for a tropical harrier, and substantial brood reduction occurred. We suggest that the relatively unusual diet for harriers comprised mainly of insects may have stimulated sibling aggression among nestlings.

In Ambohitantely Special Reserve, the topography of the area has led to irregular formation of marshes and valleys, thus restricting the nesting area for Madagascar Harriers. On the other hand, the aggressiveness of males toward conspecifics also seemed to result in the spacing of nesting pairs. Grasses, herbaceous vegetation and dry branches, from *Pinus* and *Eucalyptus* spp. trees, were utilized for nest construction by the harriers, same as reported by Paverne (1997) in Madagascar. Madagascar Harriers placed nests on grass tufts in marshes, which facilitated nest construction, similar to other marsh harrier species (Simmons 2000). The Madagascar Harrier nests were about 40 cm above the water level.

In Réunion, a small island 700 km east of Madagascar, the Réunion Harrier, a sister species to the Madagascar Harrier, began the breeding season at the same time as the Madagascar Harrier with courtship displays in August–September, nest building in October–November and onward, egg laying from January–April, and fledglings reported with adults up to October (Bretagnolle et al. 2000). Compared to the Madagascar Harrier, the Réunion Harrier had a prolonged breeding season. Harriers in Madagascar at Ambohitantely Special Reserve, commenced breeding with courtship beginning in August–September, and nest construction and egg laying in September–October, at a time when the water level in marshes was at its minimum. Paverne (1997) also had two nests underway in September and one in November 1996, in the same general region as Ambohitantely. Paverne (1997) reported on two nests with four and two eggs each, and one with undetermined number of eggs or young. We suspect the nest located in November (Paverne

1997) might possibly have been a renesting attempt due to the timing of the incubation period we recorded and the second nesting attempt we documented. By the time the rainy season began in late November and December, and water level in the marshes began rising, young harriers had fledged (first flights) or were near fledging. For the Réunion Harrier, fledging appeared to occur from March–June, and much later than our observations for Madagascar Harriers.

For Madagascar Harriers, hatching success averaged 61% for both years, and was extremely low (37%) during the 1998 breeding season due to grassland fires destroying several nests and the presence of addled eggs. The female fed and cared for the first-hatched nestling immediately, and we believe this led to a decrease of incubation time of the remaining eggs, possibly causing the high incidence of addled eggs (39%).

Simmons (2000) showed that all harrier species exhibit reverse size dimorphism, and we found Madagascar Harrier females have one of the largest body sizes, at 850–910 g, of the 16 harrier species found in the world.

Probably due to limited food and aggressive behavior from the first-hatched nestling, the second and third hatched young died at 35 and 10 d of age ($N = 2$ nests), respectively. The weakest young were killed by the first-hatched nestlings, similar to many other raptors living in food restricted environments (Meyburg 1974, Simmons 1988, Gargett 1990). Brood reduction is well documented for other harrier species as well (Simmons 2000).

Previous reports on the food habits of the Madagascar Harrier came from four stomach contents examined by Rand (1936), who found the head and feet of a Madagascar Partridge (*Margaroperdix madagascarensis*), a rat (*Rattus* sp.), fur of a small mammal, two frogs, a young whistling duck (*Dendrocygna* sp.), and an insectivorous mammal.

In Ambohitantely Special Reserve the grasslands and low-lying marsh valleys support a dense insect population of grasshoppers (*Nomadacris septemfasciata*) and provide habitat for snakes and savannah birds. Grasshoppers were the predominant prey taken by frequency, but in terms of biomass birds, reptiles, and mammals made up 90% of the harrier diet.

The Madagascar Harrier is categorized as a vulnerable species (BirdLife International 2000). In Ambohitantely Special Reserve, and most likely throughout Madagascar, there are three major human-caused threats toward this species. First, adults are persecuted for food and as a threat to domestic fowl. In one case in 1996, Randriamanga (2000) met a poacher who had displayed carcasses of 13 Madagascar Harriers he had killed. Local people also consume the eggs and nestlings as a source of protein (Randriamanga 2000). Second, during every dry season (April–October) the grasslands of Madagascar, especially the high-plateau region which includes the reserve, are burned by human-set fires to stimulate green growth for cattle fodder and land clearing. During this study, two harrier nests were destroyed during the incubation period by uncontrolled human set fires. In 1996, in an area near Ambohitantely, Paverne (1997) suggested a wild fire destroyed one of the harrier nests he was observing. Finally, the conversion of low-lying marshes and wetlands to rice fields for human food production reduces nesting habitat for this species. Currently, the vulnerable status of the Madagascar Harrier is justified based on threats to its habitat and its sparse distribution throughout Madagascar. This species has been recorded at a number of protected areas and national parks, but most of the protected areas have been established to preserve forested habitat and have limited grassland and wetland protection. Biologists need more information on the Madagascar Harrier population size and dynamics in order to provide conservation strategies and protect it in the future.

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